

**HAPLOCHELIDAE, A NEW FAMILY OF CRETACEOUS BEETLES
(COLEOPTERA: MYXOPHAGA) FROM BURMESE AMBER**

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Abstract.—A new family, genus and species of flightless beetles (Coleoptera: Lepiceroidea: **Haplochelidae: Haplochelus: *Haplochelus georissoides***) are described from Cretaceous Burmese amber. *Haplochelus georissoides* is the first fossil that can be reliably placed in the suborder Myxophaga. The new family is characterized by its small size (under 2 mm in length), long frons (extended anteriorly far beyond eyes), ventrally displaced, declined and reduced mouthparts, 7-segmented antennae with a triangular terminal club bearing a dense layer of setae, long mesosternum, very short metasternum, fused elytra with no evidence of a suture, and 1-segmented tarsi with a single and long claw terminating all legs. The new species has similarities with members of the extant *Lepicerus* Motschulsky, 1855, although it is distinct enough to be placed in a separate family.

Key Words: Haplochelidae, new family, *Haplochelus*, new genus *Haplochelus georissoides*, new species, Lepiceroidea, Myxophaga, Burmese amber, Lower Cretaceous

A small beetle with unique characters unknown in any extinct or extant family was discovered in Cretaceous Burmese amber. It is described here and its affinities within the Coleoptera are discussed. Amber from Burma (Myanmar) occurs in lignitic seams in sandstone-limestone deposits in the Hukawng Valley. Palynomorphs obtained from the amber beds where the fossil piece originated have been assigned to the Upper Albian (~ 110–100 mya) (Cruickshank and Ko 2003). Nuclear magnetic resonance (NMR) spectra of amber samples taken from the same locality as the fossil indicated an araucarian (possibly *Agathis*) plant source (Lambert and Wu, personal communication).

MATERIALS AND METHODS

The amber was polished in order to better view the specimen. The amber piece con-

taining the fossil is roughly rectangular in outline, measuring 14 mm long, 8 mm wide, and 1 mm in depth. The specimen is well preserved and complete, although some portions of the legs are obscured by the dark under portion of the body and portions of the abdomen appear to be somewhat distorted. Observations, drawings, and photographs of the fossil were made with a Nikon SMZ-10 R stereoscopic microscope and a Nikon Optiphot TM compound microscope (with magnifications up to 650×). All measurements are in mm unless otherwise noted.

Lepiceroidea Hinton, 1936

This superfamily is proposed here to include the Lepiceridae, including two extant species of the genus *Lepicerus* Motschul-

sky, 1855 (Lepiceridae Hinton, 1936 = Cyathoceridae Sharp, 1882) and Haplochelidae, n. fam. with one extinct species described below.

Diagnosis.—This superfamily differs from the Sphaerioidea in the characters listed in the key below as well as in the following features: (Sub) sinuated lateral contour of elytra, subhorizontal epipleura rather wide, with deep excision for reception of posterior legs, medial portion of anterior pronotal rim strongly projecting forward; and short intercoxal process on prothorax (not extended behind middle of procoxae). The lateral view of members of the Lepiceroidea is quite characteristic due to the peculiar shape of the head and the heightened distal part of elytra, the apices of which are strongly curved downwards (beyond the ventral plane of body).

Haplochelidae Kirejtshuk and Poinar, new family

Description.—Body small, under 2 mm in length, with rather convex dorsum; subflattened ventrally; dorsal integument with very coarse irregular sculpture, represented on elytra by somewhat regular tubercles and dense fossae, impunctate and scarcely pubescent; underside with coarse, rather dense fossae and very large punctures, lacking visible pubescence; frons anteriorly oriented, rather long (extended anteriorly far beyond eyes) and declined ventrally; mouthparts reduced, dislocated ventrally, concealed; gula comparatively narrow and deeply excavate; ocelli absent; antenna 7-segmented, with ultimate antennomere subtriangular, widest at subtruncate apex; all coxae small, apparently oval and rather narrowly separated; thorax with very long mesosternum, rather short metasternum; legs moderately raised, with distinct trochanter and spinose tibiae, tarsi 1-segmented, long and straight, with a large terminal, scarcely curved single claw; abdomen with 4 apparent ventrites; scutellum not exposed; elytra apparently completely fused, completely covering abdomen, with a deep longitudinal

excavation along middle and 3 longitudinal excavations lateral to median one; epipleura deeply and elongately excavate, with deep excisions for intermediate and posterior legs.

Type genus.—*Haplochelus*, n. gen.

Etymology.—Derived from the Greek *haplos* for simple, single, and the Greek *chele* for claw, referring to the single clawed condition.

Diagnosis.—The above-mentioned imaginal characters separate this family from all previously described extant and extinct beetles. In general form and many external structural characters, the fossil resembles members of the extant family Lepiceridae (Reichardt 1976), especially regarding the tarsomeres and single claw on each tarsus, the peculiar shape of the head, the characteristic excisions in the elytra for reception of the legs, and the elytral apices projecting far downwards (beyond the ventral plane of body). However the family differs from the lepicerids in the following characters: A long, narrow and very deeply excavate gula, completely fused elytra (without a trace of a suture) with faint longitudinal costae, 7-segmented antennae, coxae narrowly separated, and a very long mesosternum and a very short metasternum. In addition, the family Haplochelidae includes apterous species, while the known representatives of Lepiceridae have moderately developed posterior wings.

The following key separates the new family Haplochelidae from the adults of other families in the Myxophaga.

1. Tarsi 1-segmented, terminating in one claw; mouthparts dislocated ventrally; ultimate antennomere much larger than preceding ones; pronotum widened anteriorly; dorsum coarsely sculptured and without distinct punctuation; superfamily Lepiceroidea 2
- Tarsi 3- or 4-segmented, terminating in two claws; mouthparts oriented apically; ultimate antennomere of various shapes, but never much larger than preceding ones; pronotum widest at base and more or less gradually narrowing anteriorly; dorsum var-

- iable in sculpture and punctation; superfamily Sphaerioidea 3
- 2(1). Elytra with distinct suture and distinct longitudinal costae; scutellum clearly exposed; gular sutures widely separated and gula not excavate; protrochanter rather transverse and moderately developed; antenna 4-segmented; prosternal process rather wide; meso- and metacoxae moderately separated; mesosternum moderately short and markedly shorter than metasternum; pronotum with distinct anterior and posterior angles Lepiceridae
- Elytra completely fused, without trace of suture; without longitudinal costae (except for a rather sharp ridge at distal third); scutellum scarcely exposed; gular sutures rather narrowly separated and gula deeply excavate; protrochanter narrow and rather long; antenna 7-segmented; procoxae not separated by prosternal process; meso- and metacoxae narrowly separated; pronotum with rounded anterior and posterior angles Haplochelidae, n. fam.
- 3(1). Tarsi tetramerous; metacoxa without femoral plates; abdomen with 4–5 ventrites; elytra with longitudinal furrows (recent forms in Western hemisphere) or rarely without (recent forms in South Africa and southeastern Asia); legs comparatively long with rather narrow subparallel-sided tibiae Torrindicolidae
- Tarsi trimerous; metacoxa with femoral plates; abdomen with 3 or 6–7 ventrites; elytra without longitudinal furrows; legs not long with somewhat dilated tibiae 4
- 4(3). Abdomen with 3 ventrites; metacoxae large and contiguous; elytra completely covering abdomen; antenna 11-segmented with 3-segmented club; hind wing with “oblongum” Sphaeriusidae
- Abdomen with 6–7 ventrites; metacoxae smaller and more or less separated; elytra not complete and leaving apex of abdomen uncovered; antenna 5–8 segmented with 1-segmented club; hind wing without “oblongum” Hydroscaphidae

***Haplochelus georissoides* Kirejtshuk and Poinar, new species**
(Figs. 1, 2, 4–10)

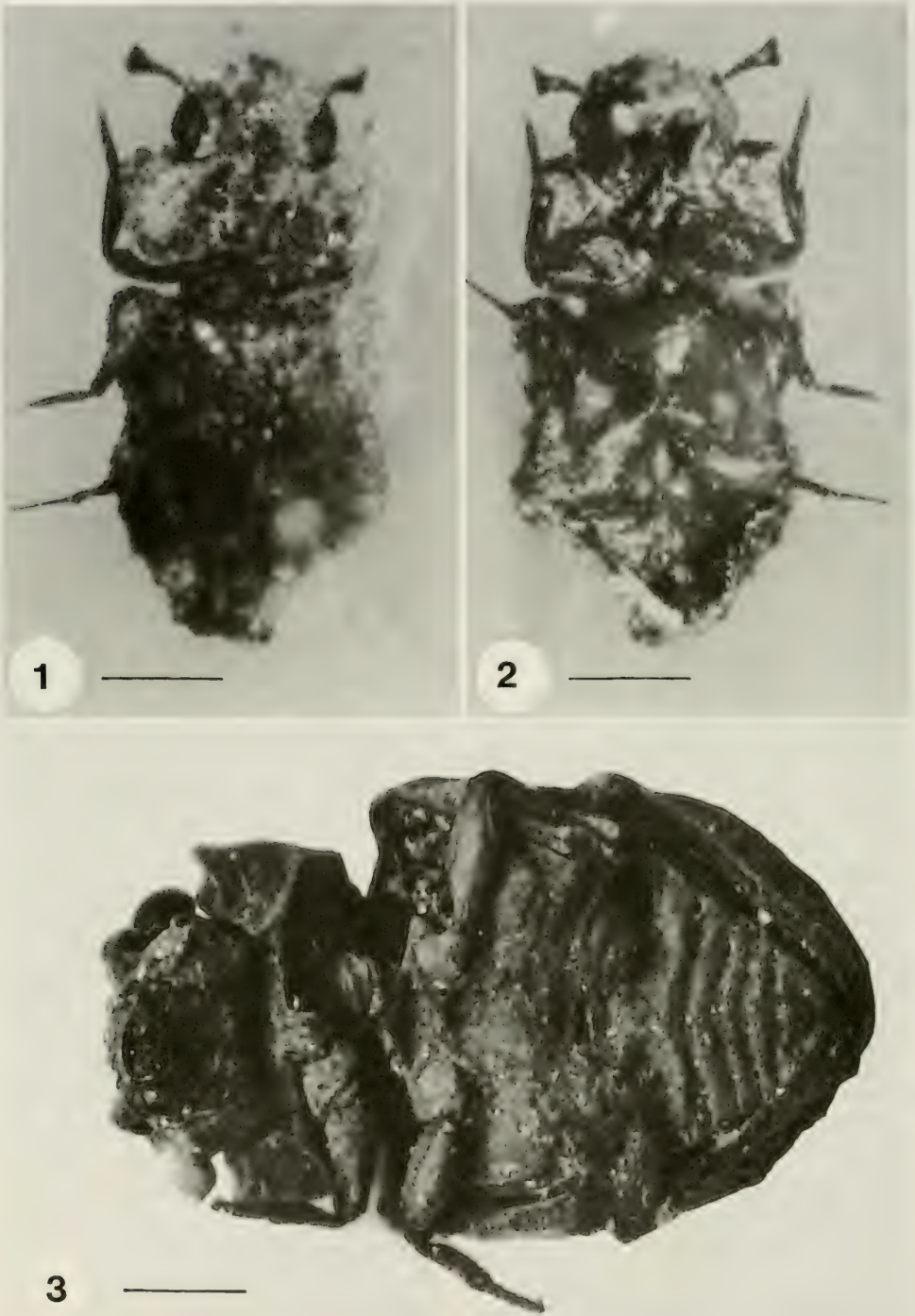
Description.—With characters listed under the family description. Length 1.43; width 0.6, height nearly 0.3 (with most height at distal third of elytra); elongate-oval, moderately convex dorsally and subflattened ventrally; dull; dorsum with extremely coarse sculpture; dorsum mostly without pubescence, with minute and partly curved bristles in some areas (particularly along lateral edge in distal half of elytra); dorsum subunicolorous dark (to blackish), due to apparent vesicles associated with sculpture in some areas (mostly along middle), appearing as light grayish; punctures absent; head and pronotum with irregular coarse sculpture; elytra with variously sized, dense tubercles (often rather protuberant) and fossae (very large punctures); venter subunicolorous blackish with coarse and rather dense fossae on prosternum, hypomera and ventrites; underside without pubescence.

Head length 0.330; width 0.360; head transverse, widely and deeply excavate, porrect with mouth directed ventrad (invisible from above) on short prolongation; with explanate expansion over each antennal insertion; two small, elongate paramedial bosses in distal half; eyes moderately developed, consisting of facets 12–14 μm in diameter; anterior part of frons strongly declined ventrally (“subvertically”); genae rather wide, excavate, declined ventrally (forming lateral walls resulting in narrow and deep gular excavations); labrum very short and wide, apistognatously oriented; mouthparts invisible except for small, narrow apices of mandibles exposed at sides of transverse apex of labrum and apparently transverse apex of rather small mentum; antenna with 7 antennomeres; scape and pedicel subcylindrical and approximately of equal length, most of scape obscured; antennomeres 3–6 subsquare or strongly transverse; ultimate (7th) antennomere

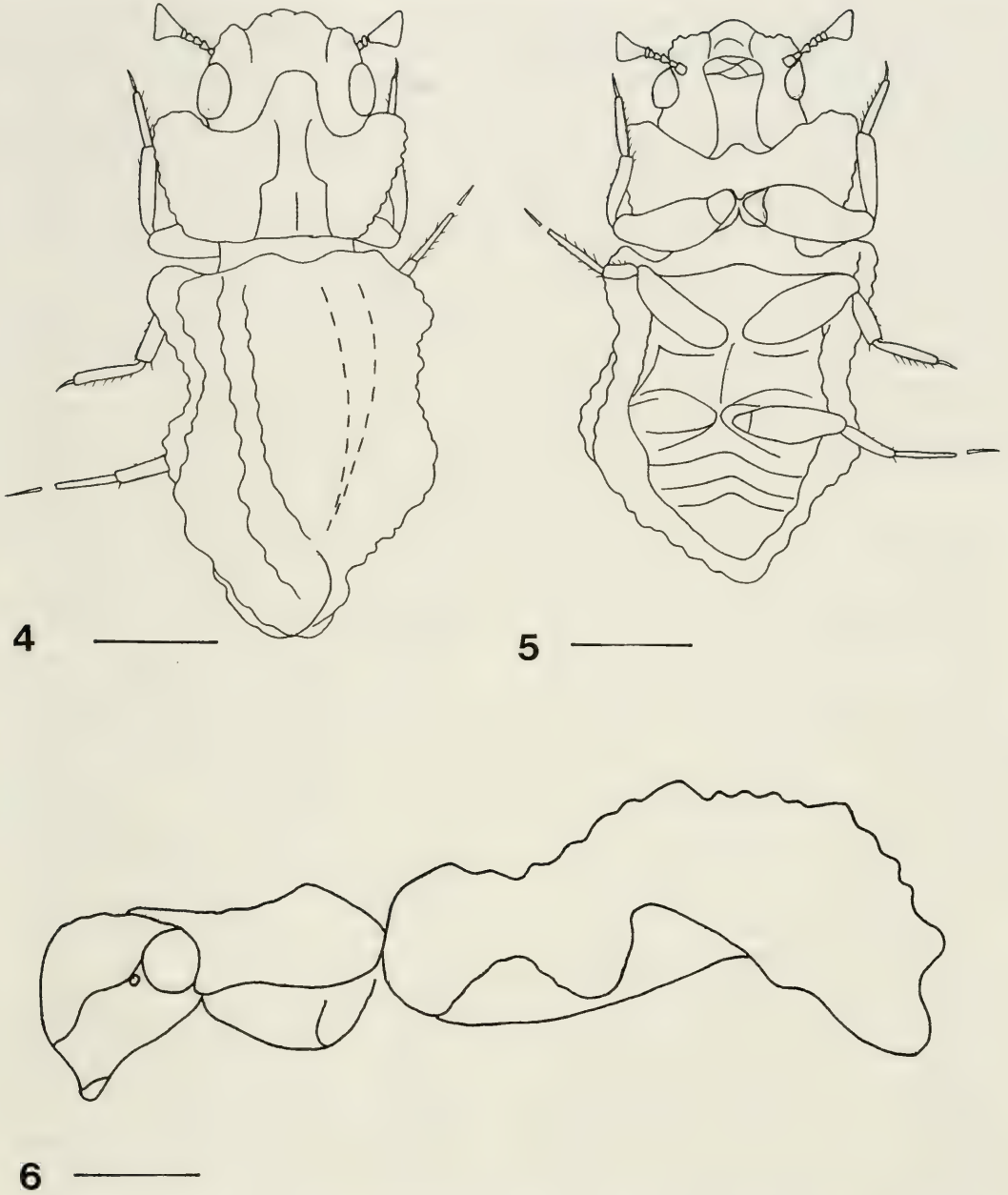
***Haplochelus* Kirejtshuk and Poinar, new genus**

This genus is represented by a single species, and therefore its description overlaps with the description of the species (“*descriptio generica specifica*”). The gender is masculine.

Type species.—*Haplochelus georissoides*, n. sp.



Figs. 1-3. Lepiceroidea. 1, Dorsal view of holotype of *Haplochelus georissoides* in Burmese amber. Bar = 280 μm . 2, Ventral view of holotype of *Haplochelus georissoides* in Burmese amber. Bar = 280 μm . 3, Ventral view of *Lepicerus inaequalis* (photo by Peter York). Bar = 277 μm .



Figs. 4-6. *Haplochelus georissoides*. 4, Dorsal view. Bar = 250 μm . 5, Ventral view. Bar = 298 μm . 6, Lateral view. Bar = 187 μm .

greatly enlarged, club-shaped with obliquely truncate apex appearing transverse; oval surface covered with diffuse, long hairs; length of antennomere 7 (club) = 75 μm ; length hairs on club, 11 to 31 μm ; antennal grooves and ocelli absent.

Thorax length 0.37, width 0.61; pronotum strongly transverse, with anterior crest over head; widest at anterior $\frac{1}{3}$, rather convex medially in posterior third and very widely excavate at sides; both anterior and posterior angles widely rounded; anterior

edge bisinuate with median part far extended anteriorly and covering considerable part of head; prosternum with hypomera forming subflattened plane; anterior wall with comparatively small, but distinct depressions for reception of ultimate antennomere; prosternal process very short and narrowing between bases of coxae; procoxa rather large and convex, trochanter elongate and comparatively long; procoxal cavities apparently contiguous; mesosternum comparatively long (somewhat longer than prosternum), slightly convex; mesocoxal cavities subcontiguous and closed laterally, appearing oval; metasternum very short (about as long as prosternum), subcarinate and with submesocoxal lines deviating from median part of coxal cavities; metacoxae apparently oval, rather small and narrowly separated; scutellum invisible; legs moderately developed; tibiae rather narrow, dorsoventrally compressed and subparallel sided, somewhat narrower than ultimate antennomere, with few small setae along outer edge and few diffusely spread short hairs; femora rather robust and of usual shape, 2–3 times as wide as tibiae, with convex anterior and posterior edges; single tarsomere of each leg very long and somewhat compressed (slightly shorter than corresponding tibia), gradually narrowed, without setose lobes, but with few short setae; unique claws very slightly curved; claw of anterior and intermediate legs about $\frac{1}{4}$ as long as corresponding tibiae; claw of posterior leg nearly $\frac{1}{3}$ as long as corresponding tibia.

Elytra fused, strongly excavate medially in anterior $\frac{2}{3}$ with strongly vaulted spaces between middle and lateral edges appearing as raised paramedial rollers with sculpture somewhat longitudinally oriented; part of elytral plane turned downward and forming a deeply concave stripe along lateral edge of elytra; excisions for reception of intermediate and posterior legs rather deep; epipleura rather distinct and subhorizontal to sloping downwards laterally before apices of elytra; a sharp keel located in place of elytral suture.

Abdomen length 0.87; width 0.60; middle of abdomen clearly vaulted along entire length, right side of abdomen distorted, especially near apex; 4 ventrites exposed (actual number of ventrites unclear because of a milky deposit); ventrite "1" longer than either ventrites "2" and "3"; apex of hypopygidium curved strongly ventrad, narrowly rounded; elytra fused, without evidence of suture.

Material examined.—Holotype in Burmese amber, deposited in the Poinar amber collection (accession # B-C-21) maintained at Oregon State University. From lignitic seams in sandstone-limestone deposits in the Hukawng Valley, Myanmar (Burma).

Etymology.—The species epithet "*georissoides*" refers to the resemblance of the new species to members of the genus *Georissus* Latreille (Coleoptera: Polyphaga: Georissidae).

Diagnosis.—The fossil has some resemblances to members of the family Lepiceridae, which is represented by two recent species, *Lepicerus inaequalis* Motschulsky, 1855 (Fig. 3) from Mexico, Panama, Costa Rica, Guatemala, and Venezuela (Reichardt 1976) and *Lepicerus bufo* (Hinton 1933) from Mexico. Reichardt (1976) synonymized *Lepicerus inaequalis* and *Cyathocerus horni* Sharp, 1882, but Beutel (1998) considered them separate.

In addition to the diagnostic characters in the above key and in the family diagnosis which separates the Haplochelidae from the Lepiceridae and other families in the Myxophaga, the following characters of *Lepicerus* that differ from those in *H. georissoides* are: Markedly more convex body, metasternum about twice as long as mesosternum, metasternum with deep median fossa at its anterior edge; metepimeres with deep groove (outlined by keel) for reception of mesotibia; prosternum shorter than mesosternum; mesocoxae about as widely separated as width of femora; metacoxae widely separated; metacoxae subtransverse and rather oblique; protrochanter transversely oblique; meso- and metatrochanters appear-

ing as very small triangles; abdomen with deep groove (outlined by keel) for reception of metafemur on ventrite 1 and metatibia along edge of ventrites 1–4; ventrites 1–4 vaulted along their posterior edges; hypopygidium with elevated oval median plate at base with dense sensilla or median protuberance; very wide gula lacking excavations; and underside of head with very deep antennal grooves below edge of eyes (continuing to lateral depression at anterior angle of pronotum).

DISCUSSION

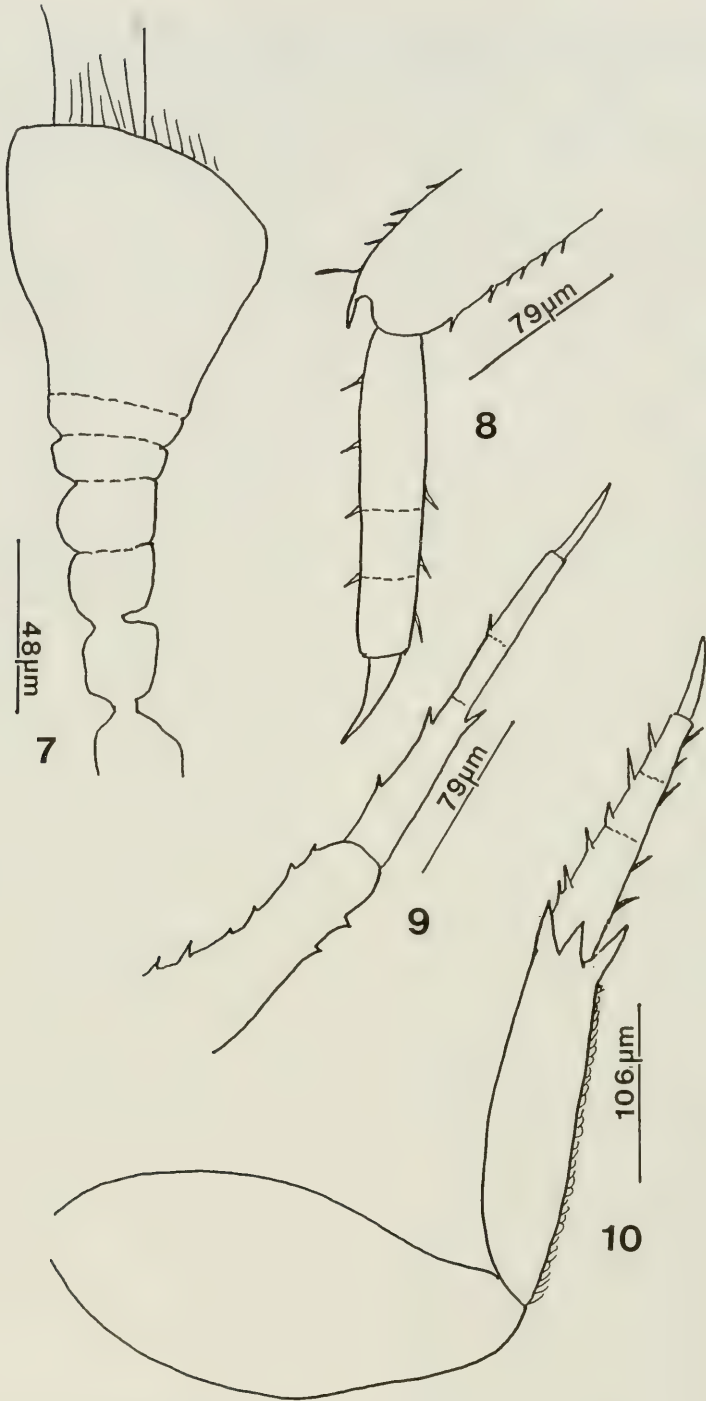
Crowson (1955) originally proposed the suborder Myxophaga as a tentative group with the single superfamily Sphaerioidea including four families of extant beetles. The basis for the recognition of this suborder was that members of these families differed from the Adephaga and Polyphaga (and also Archostemata) in venation and the manner of folding their hind wings. The Myxophaga has been recognized by many workers as “primitive coleopteron” closer to the Polyphaga or Polyphaga + Adephaga (see discussions in Reichardt 1973 and Ribera 1999). Ponomarenko (1973), based on the work of Forbes (1926), regarded this unique type of venation and wing folding as reliable evidence of a basic diversification of the order. After examining some extinct beetles dating back to the Paleozoic, Ponomarenko (1973, 2001) divided the Mesozoic and Cenozoic groups of the order into an “oblongum” lineage, (those containing a special closed cell formed by cross veins connecting the M and CuA veins in the hind wing), which included the Adephaga, Myxophaga, and Micromalthidae and a non-“oblongum” lineage. The latter group consisted of the remaining families of beetles (part of the Archostemata [sensu Crowson 1975 and Kirejtshuk 1992]) and the Polyphaga. This grouping is practical even though the hind wings of the Torrincolidae (Myxophaga) lack an “oblongum”. Kukalova-Peck and Lawrence (1993) also illustrated a similarity between the wing ve-

nation of Myxophaga and archaic forms of Adephaga and *Micromalthus* Le Conte. Recently Maddison et al. (1999) obtained evidence from ribosomal DNA sequences showing a certain affinity of the Myxophaga to the Adephaga. Ponomarenko (1973, 2001) considered that the recent groups of Myxophaga could have arisen from some groups of the schizophoroid lineage of “Archostemata” sensu Ponomarenko (1969). Nevertheless, Fedorenko (2005) felt it was not possible to link the Myxophaga and Polyphaga and that the schizophoroid lineage represents only extant groups, while the Myxophaga seem to share more characters with the Adephaga rather than with any other known group of the order.

Sharp and Muir (1912) regarded the tegmen of *Lepicerus* as similar to that of the Trogossitidae and Reichardt (1976) noted that the genitalia of *Lepicerus* differs from that of other Myxophaga. Yet the single lobed maxilla and hind wing venation were considered good arguments for placing Lepiceridae in the suborder Myxophaga (Forbes 1926, Reichardt 1976). Hlavac (1975) supported this affinity based on the structure of the prothorax, although he did not mention any specific characters that distinguished the myxophagan prothorax from those of the other suborders.

A single claw on the imaginal tarsus is found not only in the Myxophaga, but also in some weevils in the subfamilies Baridinae, Ceutorhynchinae and Entiminae, even though other members of the same subfamilies possess paired claws. Another characteristic of some Myxophaga is a “primitive number and type of Malpighian tubules” (Reichardt 1973), as is characteristic of many Polyphaga. The Myxophaga also exhibit structural miniaturization or pedomorphic characters, such as reduced number of antennomeres, unilobed maxilla, reduced number of tarsomeres, shortening of the elytra, reduction of epipleura and an abdomen with 5 ventrites.

The known larvae of Myxophaga have a greater number of structural similarities



Figs. 7-10. *Haplochelus georissoides*. 7, Right antenna. 8, Mesotarsus. 9, Protarsus. 10, Posterior leg.

with those of most Polyphaga, which has been used by some to link the two groups. However, since the larvae of many Adephaga are not primary, the many structural similarities of archostematan, myxophagan, and polyphagan larvae can be regarded as examples of larval “desembryonization” in the Holometabola in general (Tikhomirova 1991, Kirejtshuk 2000). In this interpretation, the larval similarities are regarded as plesiotypic, while the more structurally differentiated larvae of Adephaga and Staphylinoidea arose secondarily.

Extant Myxophaga are associated with algae and mosses on stones in running fresh water. The fine water droplets in the amber adjacent to *H. georissoides* suggest a moist environment. It is possible that the fossil lived among mosses and algae growing on the bark or at the base of the amber producing tree. The larvae of Lepiceridae and Haplochelidae are unknown.

The fossil record of the Myxophaga is extremely poor. Ponomarenko and Kirejtshuk (2004a, b) found an undescribed fossil imprint from the Lower Triassic, which was preliminarily placed into this suborder, however these remains should be studied more carefully. *Haplochelus georissoides* is the only fossil representative that can reliably be placed in this suborder.

The superfamily Lepicerioidea shows a tendency for reduced adult mouthparts. This feature can be interpreted as evidence that imaginal feeding among representatives of the superfamily was not that significant. While the head is distinctly prognathous with lateral lobes expanded anterolaterally over the antennal insertions, the mouth orifice is oriented ventrally (particularly in *H. georissoides*) which is peculiar among Coleoptera.

The general shape of the lepiceroid elytra also is not typical among beetles. Both *Haplochelus* and *Lepicerus* show more or less expressed sinuations at the midsides of the elytra and rather wide and subhorizontal complete epipleura with depressions for the reception of femoro-tibial articulations.

However, while *Lepicerus* has longitudinal ribs with punctuation on separated elytra, the fused elytra of *Haplochelus* bear subuniform and coarse sculpture, with only a trace of punctuation. Another structural peculiarity of the Lepicerioidea is the characteristic shape of the pronotum, which is widened anteriorly with the median portion of the anterior part extended over part of the head. Such a condition is unusual, although it occurs among different groups of the suborder Polyphaga, particularly in the Tenebrionoidea and Phycosecidae (Cleroidea). Species of *Phycosecis* Pascoe also have thoracic sclerites somewhat similar to those in *Haplochelus georissoides*, but these beetles are very different in many other structural characters (Matthews 1992).

Some apterous species of the Tenebrionoidea and Curculionoidea have a shortened metathorax, however, in contrast to *Haplochelus georissoides*, this shortening includes an elongation of the mesothorax. A shortening of the metathorax might be expected in apterous species, at least in those in which the condition is quite ancient.

ACKNOWLEDGMENTS

The senior author was supported by the Presidium of the Russian Academy of Sciences in the Programme “Origin and evolution of biosphere” and by a grant of the Royal Society that allowed him to visit The Natural History Museum, London, in 2005. We thank M. Barclay and Peter York, The Natural History Museum, London, for their assistance in obtaining figures (originally photographed by Harry Taylor in this museum) of *Lepicerus inaequalis* from the D. Sharp collection. We also express thanks to N.B. Nikitsky from the Zoological Museum at the Moscow State University for his assistance in obtaining the type specimen of *L. inaequalis* from the V. Moschulsky collection. Grateful appreciation is extended to Alex Brown for his assistance in obtaining the fossil specimen. We thank two anonymous reviewers for their helpful comments.

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